

Introduction to the symposium “Molluscan models: Advancing our understanding of the eye”*

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Since the time of Darwin, the eye has been a subject of evolutionary and comparative biologists alike who were intrigued by the structural complexity and morphological diversity of eyes in nature. Much of what we know about the eye—development, structure, physiology, and function—has been determined from only a handful of model organisms, specifically the mouse and the fly. One major phylum in particular, the Mollusca, has been underutilized in investigating the evolution and development of the eye. This is surprising as molluscs display a myriad of eye types, such as simple pit eyes without any apparatus to focus images, compound eyes that superficially resemble the eyes of flies, camera-type eyes that are similar to vertebrate eyes, and eyes with mirrors, just to name a few. As a result, molluscan eyes comprise more morphological diversity than seen even in the largest animal phylum, the Arthropoda.

With all of this incredible diversity, how do we as researchers determine which mollusc species should be developed as models to study the eye? Serb provides background for eye research using traditional model organisms and how using molluscan species would be advantageous to understanding the eye. She describes the research potential of molluscan species as model organisms and identifies criteria that might be used to develop a molluscan model and the questions molluscan models might address.

One application of molluscan models is to study the cellular biology of human eye disease. As many degenerative eye diseases, such as macular degeneration, have been linked to the mis-organization of the cytoskeleton within retinal cells, understanding the control of cytoskeleton organization and its influence on photoreceptor cell changes may lead to prevention and possible cures for some eye diseases. Gray, Kelly, and Robles utilize *Octopus bimaculoides* Pickford and McConnaughey, 1949 as a model organism to study the molecular controls of cytoskeleton organization in the retina. Their work identifies a cell signaling path-

way (Rho GTPase) that mediates cytoskeleton rearrangements. Errors in this pathway may prove to be one of the factors that disrupts cytoskeleton formation, leading to retinal degeneration.

After developing one or several molluscan models of the eye, how does one set about understanding this great diversity of eyes and place it in an evolutionary context? One way is to use a comparative approach to identify conserved and variable components of eye morphology, such as lens composition, photoreceptor number and organization, and overall eye shape. These morphological features can provide evidence for functional differences and visual capabilities among species. Several authors in the symposium take this approach. Speiser and Johnsen examine eye morphology in four species of scallop and a closely related spondylid (*Spondylus americanus* [Hermann, 1781]). They show that scallop eye structure varies among species, and these structural differences affect optical resolution and sensitivity. Further, they provide evidence that actively swimming species (e.g., *Amusium balloti* [Bernardi 1861]) have better optical resolution than non-swimming species. Speiser and Johnsen provide several new and exciting hypotheses on how the scallop eye performs and how visual requirements may differ between mobile and immobile species. Morton takes a broader perspective and reviews the diversity of non-cephalic eye types in the Class Bivalvia. He hypothesizes a possible evolutionary path to create the double retina system in Pectinidae and Laternulidae through the duplication of sensory structures on the pallial folds. Zieger and Meyer-Rochow review the variation of cephalic gastropod eyes, concentrating on pulmonate species, which are the best-studied eyes in gastropods. They discuss eye anatomy, differences in retinal design, and the visual capabilities of different optical components. Finally, they describe the ultrastructure of “additional” or “accessory” eyes associated with cephalic eyes in several lineages. These data provide

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hints of the function of these structures and indicate behavioral experiments to test these hypotheses.

A comparative approach also can be used to examine changes in development, not just morphological endpoints. For example, even though most gastropods have eyes, loss of eyes occurs in some eyed lineages. Often eye loss is associated with dark environments, such as abyssal depths or caves, but little is known of when or how eye loss occurs. Averbuj and Penchaszadeh show that eyes are present in the "eyeless" genus *Buccinanops* (d'Orbigny, 1841) (Caenogastropoda: Neogastropoda) during the encapsulated larval stage. What happens to these cephalic eyes post-hatching is unknown, but why have eyes in non-motile larvae? Do other "eyeless" species have eyes as larvae and lose those eyes after the veliger stage? Studying these and other "eyeless" taxa may provide data on the evolutionary constraints of development on morphology. This is a promising area for future research.

Another way to study the eye is to examine differences among the various components that comprise the organ. Eyes are not just single, irreducible entities but they contain levels of biological complexity nested in a hierarchical fashion (e.g., Serb and Oakley 2005). Therefore, the eye can be subdivided into components, or modules, such as genetic networks (i.e., *Pax6* network), photoreceptor cell types, crystallin proteins that make up the lens, photo-transduction pathways that convert light into a chemical signal, and the eye itself as a morphological structure. Several authors focus on specific eye modules.

One module consists of crystallin proteins, which form the lens in both vertebrate and invertebrate eyes. Evidence indicates that these proteins initially performed biochemical functions unrelated to vision and were later recruited for optical purposes during the evolution of the eye lens (Cvekl and Piatigorsky 1996). In the symposium, Piatigorsky discusses the origin and evolution of lens crystallins in cephalopod and bivalve molluscs via processes of gene recruitment, gene sharing, and gene duplication.

Other eye components are the light-sensitive cells, photoreceptors, which are ubiquitous in animal eyes. Salvini-Plawen presents an interesting hypothesis on the evolution of the major classes of animal photoreceptors. He suggests that despite the structural differentiation of ciliary *versus* rhabdomeric photoreceptor cells, these cells are not distinct classes, but the result of ontological changes of a single cell type. Support for his hypothesis includes a comprehensive treatment of molluscan photoreceptor diversity. Wilkens examines the physiology of photoreceptors in bivalves—specifically, how do photoreceptor cells respond to light and how is this information processed outside of the eye? Based on physiological and behavioral work, he describes differences between species and among photorecep-

tor cell types within a single eye. Finally, he hypothesizes the functions of bivalve eyes.

In addition to these published papers, other symposium participants presented work on a range of topics. Eernisse reviewed the sensory system of chitons (Polyplacophora) and discussed how the recent appearance of chiton ocelli may have evolved in parallel in two phylogenetically distant lineages. Kelly and Robles (Kelly *et al.* 2008) added to the work of Gray *et al.* to identify a translational regulation mechanism for cytoskeleton proteins that have differential expression in light- versus dark-adapted octopus eyes. Speiser and Johnsen (2008) experimentally show that scallops use visual cues to adjust feeding behavior relative to the movement and size of particles suspended in the water.

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